THE REACTION OF CERTAIN CRUSTACEA TO DIRECT AND TO DIFFUSE LIGHT

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Many plankton organisms which move downward, away from daylight in the sea, move toward a source of light in the laboratory. It was suggested in a previous paper (Schallek, 1942) that this behavior is caused by the animals' being exposed to diffuse light in nature, but to direct light in the laboratory. It was reported that when a tall glass cylinder containing the copepod *Acartia tonsa* was illuminated from above, the animals swam up toward the light. This phototropic reaction seemed to depend on the fact that the light was shining directly down the axis of the cylinder. But when the lamp was moved so as to illuminate the container obliquely, the refraction of the light at the surface of the water and its reflection from the curved inner wall of the cylinder seemed to form a diffuse illumination. Under these circumstances the animals sank downward, simulating their behavior in nature. The present paper provides a further development of this hypothesis based on measurement of the light distribution inside the cylinder.

Apparatus

A glass cylinder 18 inches high and six inches in diameter was used for the experiments. The cylinder was kept at 15° C. in a constant temperature bath 15 inches high and 15 × 18 inches in area. The bath had black walls to absorb reflected light, and was kept in a photographic darkroom. Illumination was from a 75-watt lamp with a parabolic, aluminum-coated reflector. The lamp was placed in five different positions, each 12 inches from the top of the cylinder, but separated by 22.5°. Position 1 was on a level with the top of the cylinder, while position 5 was directly overhead.

Light measurements were made with a Westinghouse "Photox" cell connected to a micro-ammeter, and calibrated in foot candles with a Macbeth illuminometer. The cell was placed in a waterproof case, and covered with a cylindrical hood, limiting the light received to an angular opening of 22.5°. The cell was held six inches below the surface of the cylinder by clamps and rods attached to a ringstand. As this apparatus would not fit inside the six-inch cylinder, an 11-inch cylinder was used for the light measurements. This change is not believed to be a significant source of error.

Twenty *Acartia tonsa* were placed in the cylinder at a time, while the lamp was shifted from position 1 (oblique) to position 5 (overhead). Alternate runs were made in the opposite direction. Two hours' exposure to each position was allowed before counting to permit the animals to reach equilibrium. Results are presented as the percentage of animals in the top third of the cylinder.

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Observations

A. tonsa moves down when the illumination is oblique, and moves up when the lamp is overhead (Table I). Measurements of the light distribution inside the cylinder are given in Figure 1.

TABLE I

Distribution of animals in cylinder
Average of three runs with 20 animals each

Light position	1	2	3	4	5
Elevation above horizontal	0	22.5	45	67.5	90°
			Per cent animals in top third of cylinder		
Acartia tonsa	13	29	47	65	68
Centropages typicus	69	70	72	72	79

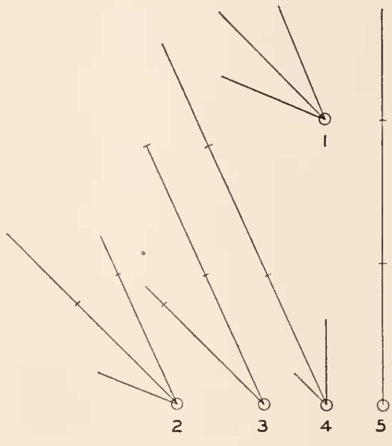

FIGURE 1. Light distribution inside the cylinder for each position of lamp. The small circle indicates the location of the photometer, six inches below the surface of the water. The number of each lamp position is given below the circle. The length of each line represents the light intensity recorded when the photometer was pointed in that direction. Logarithmic scale: the first crossbar = 100 foot-candles, the second = 1000 F. C. The hood limiting the incident light to 22.5° made the cell insensitive to less than 20 F. C.

These measurements reveal several factors that may influence the behavior of *A. tonsa:*

1. There is a 50-fold increase in the *intensity* of the maximum beam as the lamp is raised over the cylinder. It may be that the animals swim up in a bright light and sink down in a dim one. To test this factor, a slide-wire resistance was connected in series with the lamp, permitting the light intensity to be varied while the lamp was held in the overhead position. A 120-fold increase in the intensity of the light had no effect on the distribution of *A. tonsa* (Table IIA).

2. The *direction* of the maximum beam is vertical in position 5, but is more horizontal in the other positions. Perhaps the animals swim toward a vertical light but sink downward in a horizontal one. This possibility was tested by

TABLE II

Effect of changing light intensity

A. Cylinder vertical, light overhead.
Average of three runs with 20 *A. tonsa* each

Light intensity	10	200	1200 F. C.
Per cent animals in top third of cylinder	56	52	54

B. Horizontal trough, illuminated from end.

Light intensity		10	20	200	1300 F. C.
Time to move 10 inches					
Animal	1	130	150	125	130 seconds
	2	15	25	10	15

placing the cylinder on its side. The light from position 5 (shining directly down the axis of the cylinder) formerly was vertical, but now came in a horizontal direction. When the lamp was in position 1 (oblique) the animals sank downward (Figure 2A); when it was moved to position 5 (now horizontal) the animals swam to the end of the cylinder nearest the light (Figure 2B). Hence the animals swim toward the light when it is parallel to the axis of the cylinder, and sink downward when it is oblique, regardless of whether the light comes from a horizontal or a vertical direction.

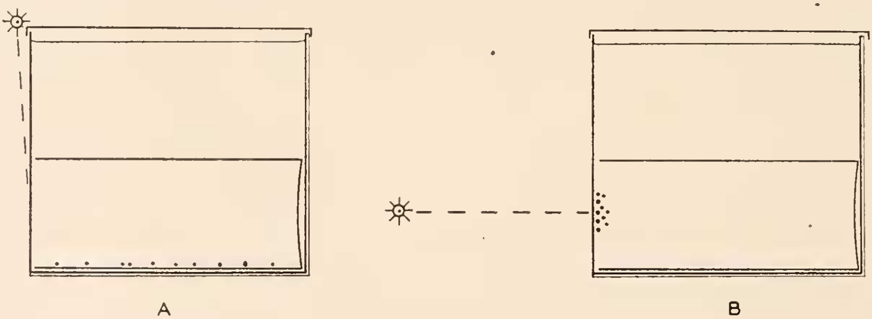

FIGURE 2. Arrangement of apparatus to test effect of light direction. A, lamp in position 1; B, lamp in position 5. Position of animals shown by black dots. The cylinder is on its side in a glass tank painted black (double line) on all sides except one through which the light enters. A piece of tarpaper covers the top.

A further test was made with a horizontal tropism trough, which could be illuminated at either end by a beam of light shining directly down the trough. *A. tonsa* always moved toward the light under these conditions; by turning on first the light at one end and then that at the other, it was possible to keep an individual moving back and forth from end to end indefinitely. Here again the reaction is independent of light intensity (Table IIB).

3. The *distribution* of the light changes as the lamp is moved. In position 5 the illumination is highly directional, with all the light coming from a single direction. In position 1 the illumination is more diffuse, the light coming almost equally from three directions. This angular distribution can be conveniently measured by the ratio (sum of intensities in other directions) : (highest intensity).

The 22.5° hood permitted 16 readings to be taken by rotating the photometer through 360°. For perfectly direct illumination, with all the light coming from one direction, this diffusion ratio will be 0 : 1, or 0. For perfectly diffuse illumination, with the light coming equally from each of the 16 directions in which measurements were made, it will be 15 : 1, or 15. The diffusion ratio for each position of the lamp is given in Table III. The curve formed by plotting these values against the percentage of animals in the top third of the cylinder is shown in Figure 3.

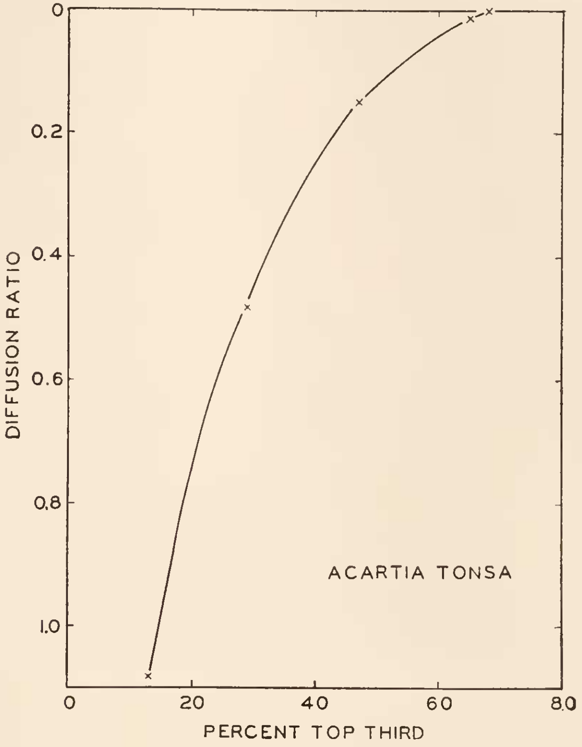

FIGURE 3. Influence of distribution of light on behavior of *A. tonsa*. Ordinate, diffusion ratio of light. Abscissa, per cent of animals in top third of cylinder.

The possibility remains that this relation is an artifact caused by the particular apparatus or procedure used. This is not so, since another copepod, *Centropages typicus*, is only slightly affected by the shift in lighting (Table I). It must therefore be concluded that the behavior of *A. tonsa* depends upon the angular distribution of the light:

1. *A. tonsa* moves toward a source of highly directional light, regardless of the intensity of the light or the direction from which it comes. This is a typical positive phototropism.

2. *A. tonsa* sinks downward in less directional (diffuse) light. This is a positive geotropism and not a negative phototropism, since the animal does not move along the beam of maximum light, but sinks passively downward.

Which of these types of illumination will animals encounter in nature? Measurements were made of light distribution in air, while the distribution of light in the sea was calculated from the data of Whitney (1941) (Figure 4, Table III).

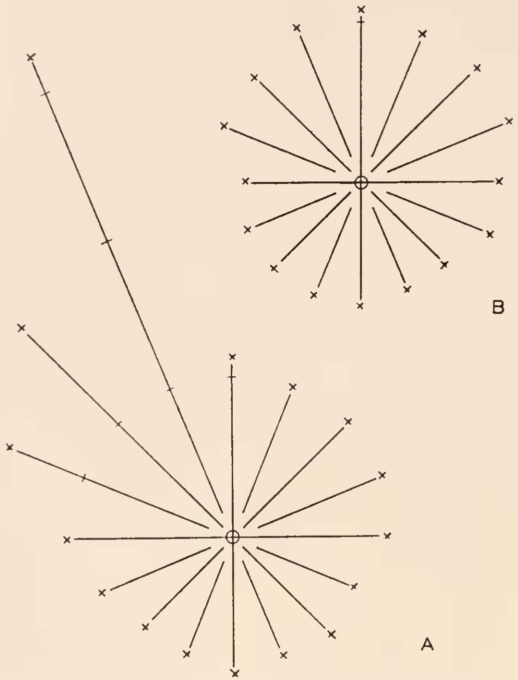

FIGURE 4. Light distribution three feet above roof of Marine Biological Laboratory. August 2, 1942, 10 A.M. Arrangement as in Figure 1.
A. Clear sky, plane of sun.
B. Clear sky, plane perpendicular to sun.

It is evident that light in the sea becomes even more diffuse than any conditions reached in the cylinder. *A. tonsa* sinks downward in diffuse light in the laboratory, and this reaction apparently accounts for the fact that it leaves the surface of the sea in the daytime (Esterly, 1928). *Centropages typicus*, which moved down only slightly in the diffuse light in the cylinder, shows only a slight downward movement in the sea (Clarke, 1934).

Discussion

There are several reports in the literature of animals which react phototropically in a horizontal tube illuminated from the end, but which sink downward in a vertical tube illuminated obliquely (Table IV). Like *A. tonsa*, these animals apparently have different responses to direct and to diffuse light. Most of them show an upward movement in the dark.

The diversity of these animals, ranging from protozoans to arthropods and echinoderms, suggests that a principle of general importance is involved. A

Table III

Summary of light measurements

$$\text{Diffusion ratio} = \frac{\text{sum of other intensities}}{\text{highest intensity}}$$

Complete concentration = 0; complete diffusion = 15

		Diffusion ratio
Measurements in cylinder *		
six inches below surface		
Light position	1	1.08
	2	0.48
	3	0.15
	4	0.012
	5	0
Measurements in sea (Whitney, 1941)		
5 met. below surface		
Clear sky, plane of sun		2.6
perpendicular to sun		3.2
Diffuse sky, any plane		2.0
Measurements in air		
3 feet above ground		
Clear sky, plane of sun		0.13
perpendicular to sun		9.2
Diffuse sky, plane of sun		6.2
perpendicular to sun		6.8

* As the hood limiting incident light to 22.5° made the photocell insensitive to less than 20 F. C., these values are probably somewhat lower than the true ones.

Table IV

Summary of geotropism experiments

Animal	Phototropism in horizontal tube	Geotropism in vertical tube		Author
		In light	In dark	
Corethra plumicornis larva	+	+	−	Harper, 1907
Cyclops albidus	−	+	−	Esterly, 1907
Branchipus serratus	+	+	−	McGinnis, 1911
Daphnia pulex	+	+	−	Dice, 1914
Sagitta bipunctata	+	+	−	Esterly, 1919
Diadema setosum larva; *Paramecium*	Indif.	+	−	Fox, 1925
Holopedium gibberum	+	+	Indif.	Kikuchi, 1938
Hemimysis lamornae	+ or −	+	−	Foxon, 1940
Acartia tonsa	+	+	−	Schallek, 1942

The nauplii of *Balanus perforatus* sink to the bottom of the aquarium when taken from the dark into horizontal light, but swim up when the lamp is moved overhead (Ewald, 1912). Indif. means indifferent.

possible explanation of this effect is provided by Clark (1933). The beetle *Dineutes* moves toward the lamp if placed in a direct beam of light. If a piece of white cardboard is held perpendicular to the beam 300 cm. behind the animal, occasional circus movements appear. These become more frequent as the cardboard is brought closer to the animal, until at 10 cm. they become continuous.

This effect is attributed to the stimulation of additional ommatidia by the light reflected from the cardboard. In concentrated light, the photoreceptor will be stimulated from the front only, and the animal will then react in a typically phototropic fashion. In diffuse light, however, the photoreceptor will be stimulated from both front and side, and a different behavior appears. In the case of *A. tonsa* this results in cessation of activity, since the animal may be observed to sink passively in diffuse light.

Laboratory studies of the light reactions of animals have largely been concerned with phototropic behavior in a direct beam of light. Measurement of the light distribution in the sea shows that it is much more diffuse than in such experimental conditions. The reaction of *A. tonsa* to diffuse light in the laboratory accords with its downward movement in the ocean during the day. Its reaction in the direct light in which experiments on phototropism are usually conducted has no bearing on its behavior in nature.

Such relations may not be confined to this particular copepod. Several reports have been quoted suggesting similar behavior in other aquatic forms. The measurements of light distribution in air show that it is generally diffuse. Perhaps this will solve the riddle of why positively phototropic insects do not fly up to the sun: they may move toward a direct light but behave differently in diffuse light. Phototropism experiments in a direct beam of light need not necessarily apply to the behavior of organisms in nature.

Summary

When the copepod *Acartia tonsa* is placed in a tall glass cylinder illuminated from above, the animal swims upward. When the cylinder is illuminated obliquely, the animal sinks downward.

Measurement of the light distribution inside the cylinder shows that the behavior of *A. tonsa* depends upon the angular distribution of the light. In highly directional illumination, the animal reacts phototropically, and swims toward the light. In less directional (diffuse) illumination, the animal stops swimming and sinks passively downward.

Measurement of the light distribution in the air and in the sea shows that it is generally more diffuse than the conditions in the cylinder. The reaction of *A. tonsa* to diffuse light in the laboratory accords with its downward movement in the ocean during the day. Its reaction in the direct light in which phototropism experiments are usually performed has no bearing on its behavior in nature.

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